GASTROPOD TORSION: A TEST OF GARSTANG'S HYPOTHESIS

J. TIMOTHY PENNINGTON AND FU-SHIANG CHIA

Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

ABSTRACT

Torsion occurs in gastropod molluscs as a 180° twisting of the shell and viscera relative to the head and foot of the veliger larva. Garstang (1928, 1929) proposed, and it has since become widely accepted, that torsion functions as a larval defense by allowing veligers to first pull the head into the shell, then sealing the aperture with the foot and operculum.

However, when we offered pre-torsional and torted larvae of the abalone *Haliotis kamtschatkana* Jonas as prey to seven planktonic predator species from four phyla, in only one case was rate of predation reduced on torted larvae. It therefore appears that torsion does not function defensively, indicating that other selective pressures probably maintained this trait in primitive gastropods.

INTRODUCTION

Gastropod torsion is a morphogenic event which occurs during larval life, and results in a 180° rotation of the shell and viscera relative to the head and foot of the veliger. Many authors have speculated about the adaptive value of torsion (Morton, 1958a), but the hypothesis proposed by Garstang (1928, 1929) remains the most widely accepted (Lever, 1979). Because torsion enables a veliger to retract its head and foot into the shell and subsequently seal the aperture with the operculum, Garstang (1928, 1929) suggested that torsion evolved as a larval defense. Garstang (1929) and several others (Yonge, 1947, 1960; Knight and Yochelson, 1958; Morton, 1958a, b; Fretter and Graham, 1962; Morton and Yonge, 1964; Purcheon, 1968; Yonge and Thompson, 1976) have proposed that torsion arose functionally complete through a single mutation. This view remains tenable because no partially torted fossil gastropods have been found (Knight, 1952; Ghiselen, 1966; Lever, 1979), and retains popularity, in part, because of the revival of saltationist evolutionary theory (*cf.* Eldredge and Gould, 1972). The defensive benefits to this torted larva were apparently great enough that it survived to become the progenitor of the Gastropoda. However, Thompson (1967) criticized Garstang's (1929) hypothesis on the grounds that the head and velum are not clearly more vulnerable to attack than the foot, and that opisthobranch veligers do not require torsion to retract completely within their shells (Thompson, 1958, 1967). Jägersten (1972) also suggested that larvae are usually swallowed whole by their predators, and that the ability to retract the head first is probably more important to adults than to larvae.

Because the torted condition persists in most juvenile and adult gastropods, Garstang (1928, 1929) further suggested that torsion in larvae may create maladaptive features for adults. It has been suggested that shell slits, pallial asymmetries and detorsion in opisthobranch gastropods have evolved, at least in part, to correct detrimental features of torsion for benthic existance (Garstang, 1929; Borradaile *et al.*, 1951; Yonge, 1960). Conversely, Garstang's (1929) hypothesis has been modified because it does
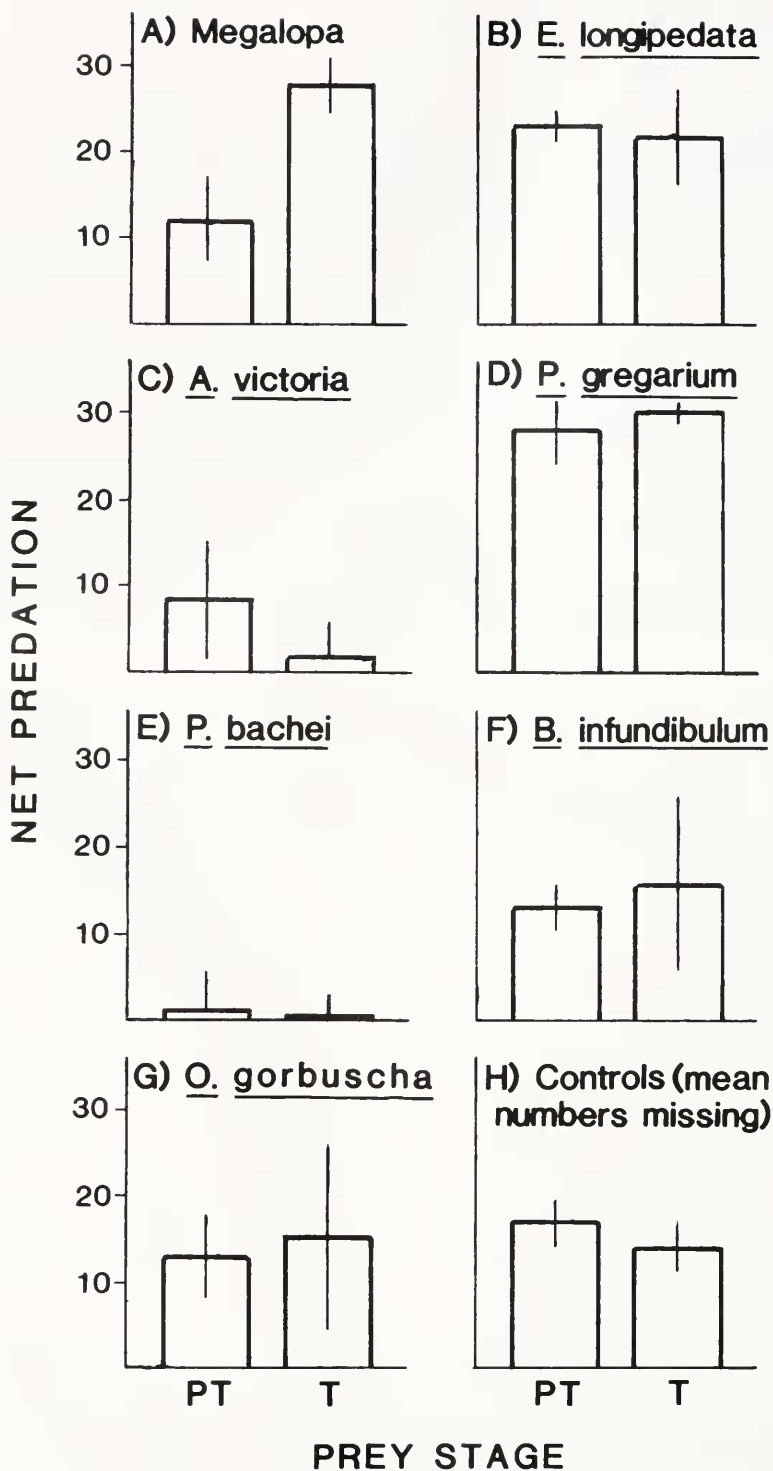
FIGURE 1. "Net predation" upon both pre-torsional (PT) and torted (T) veligers of the archeogastropod *Haliotis kamtschatkana* Jonas by seven species of planktonic predators (A–G; see text for complete descriptions of predators). Bars indicate means ± 1 standard deviation. "Net predation" was calculated by subtracting the mean numbers of veligers missing from control treatments without predators (H) from the mean numbers

not postulate advantages for benthic gastropods. Alterations of mantle position or shell size, weight, coiling, or position have all been suggested to be advantageous consequences of torsion for benthic gastropods (Lang, 1900; Naef, 1911; Yonge, 1947, 1960; Borradaile *et al.,* 1951; Morton, 1958a, b; Allen, 1963; Morton and Yonge, 1964; Ghiselen, 1966; Purcheon, 1968; Jägersten, 1972; Underwood, 1972; Solem, 1974; Lever, 1979; Stanley, 1982). To date, no experimental data have been produced to test Garstang's (1928, 1929) hypothesis, or any other proposed function of gastropod torsion.

This study was designed to test Garstang's (1928, 1929) hypothesis by comparing mortality rates of pre-torsional and torted veligers of the abalone *Haliotis kamtschatkana* Jonas, when offered as prey to an array of seven planktonic predator species from four phyla. The development of *H. kamtschatkana* has been briefly described by Caldwell (1981), and is similar to that reported for other haliotids (Crofts, 1938; Ino, 1953; Carlisle, 1962; Leighton, 1972, 1974). The pre-torsional and torted veligers used in experiments were nearly identical in size and swimming ability, though the torted veligers had undergone only the first 90° of torsion (see Crofts, 1938). At this stage, torted veligers were fully capable of retracting and sealing the shell aperture with the operculum.

MATERIALS AND METHODS

Gametes were obtained according to the methods of Morse *et al.* (1977, 1978), and embryos and larvae were cultured about 48 h (pre-torsional veligers) or 120 h (torted veligers) at 8–10°C in 3 μm filtered seawater plus 50 μg/l each of penicillin G and streptomyosin sulphate. Predators were hand-dipped from surface waters near Friday Harbor Laboratories, Washington, and used in experiments on the day of collection, or fed and maintained a few days in running seawater prior to experiments.

The experiments were similar to those of Pennington and Chia (1984) and Rumrill *et al.* (in press), which documented stage-specific predation upon other larval types. Two experiments were conducted. In the first, pre-torsional veligers were used as prey, and in the second, torted veligers were used. For each experiment 50 veligers were placed into each of 40 one-liter jars containing filtered seawater. Thirty-five of the jars were divided into seven sets of five replicates. Each jar within a set then received a predator species as follows:

(1) five brachyuran megalops larvae (Decapoda);
(2) five *Epilabidocera longipedata* (Copepoda);
(3) one 30 mm diameter *Aequorea victoria* (hydromedusa);
(4) one 12 mm diameter *Phialidium gregarium* (hydromedusa);
(5) one 10 mm diameter *Pleurobrachia bachei* (Ctenophora);
(6) one 20 mm long *Bolinopsis infundibulum* (Ctenophora); or
(7) two 30 mm long *Oncorhynchus gorbuscha* (Pisces).

No predators were added to the five remaining jars which served as controls to measure background prey mortality and handling errors.

of veligers missing from the treatments with predators. Statistics were calculated with log-transformed raw data; "net predation" was produced for graphic clarity alone. Except for *P. bachei* (E; $P > .05$), all predators ate significant numbers of prey (analysis of variance; $P < .007$ or less). However, only the megalopa (A) and *A. victoria* (C) ate significantly different numbers of either pre-torsional or torted veligers (Student-Newman-Keuls range test; $P < .05$).

During experiments, jars were strapped around the horizontal axis of a grazing wheel (see Landry, 1978; Yen, 1982), which gently stirred the water to keep the prey evenly distributed. Experiments were run for 15 h in a 7:6 h light:dark 9°C coldroom. At the end of experiments, predators were removed and prey were concentrated by siphoning most of the water off through Nitex mesh. Surviving prey were fixed, and counted later. A one-way analysis of variance and a Student-Newman-Keuls range test was calculated with log-transformed data for each predator species. These statistics tested for significant differences between control values and values for treatments with predators, and also for differences in rate of predation upon pre-torsional and torted veligers.

RESULTS

Results of the experiments (Fig. 1) show that with the exception of *Pleurobrachia bachei* ($P > .05$), all predators ate significant numbers of veligers ($P < .007$). *P. bachei* apparently did not consume veligers, though it does eat other planktonic prey in similar experiments (Pennington and Chia, 1984). Rates of predation upon pre-torsional or torted veligers were significantly different only for the megalopa and *Aequorea victoria* ($P < .05$). The megalopa consumed more torted veligers while *A. victoria* ate more pre-torsional veligers.

DISCUSSION

Except for *Aequorea victoria*, no predator species ate significantly fewer torted than pre-torsional veligers. Moreover, any advantage torsion confers to veligers against predators such as *A. victoria* is apparently offset by increased vulnerability to predators such as megalopa, and the apparent effectiveness of torsion against *A. victoria* is not general for hydromedusae, because *Phialidium gregarium* ate nearly equal numbers of both stages of prey. Our results thus do not support Garstang's (1928, 1929) hypothesis concerning the defensive value of torsion in veligers.

We have not determined why torted veligers, which have developed an operculum and can seal themselves within their shells, were as vulnerable to predation as pre-torsional veligers. Shells of larval molluscs have often been suggested to serve defensively, and several authors have even suggested that veligers can pass unharmed through the guts of their predators (Morton and Yonge, 1964; Yonge and Thompson, 1976; others reviewed by Mileikovsky, 1974). Torted veligers placed on a glass slide usually withdrew upon being disturbed for only a few seconds; perhaps this intermittent retraction was insufficient to deter predators that swallow prey whole. Empty veliger shells were often found within the manubria of *P. gregarium* at the end of experiments. Shell fragments were also commonly found within jars that had contained crustacean predators. If the crustacean predators broke shells prior to ingestion, retraction probably did not protect the larva within. Mileikovsky (1974) suggested that if veligers do pass intact through the guts of their predators, they are usually so entangled in mucous and feces that they rarely survive in any case.

The present study provides the first data to test any hypothesis concerning the adaptive value of gastropod torsion. It might be argued that over evolutionary time, small (and therefore undetected by us) decreases in rate of predation due to torsion would provide sufficient selective pressure to maintain the trait. While this argument is valid, Garstang (1928, 1929) and several recent authors (Yonge, 1947; Knight, 1952; Knight and Yochelson, 1958; Morton, 1958a, b; Morton and Yonge, 1964; Purcheon, 1968; Yonge and Thompson, 1976; Stanley, 1982) have proposed that a single mutation

caused torsion in a larval pre-gastropod whose fitness became so enhanced that it became the progenitor of the Gastropoda. Our results indicate that the defensive benefits of torsion for veligers, if any, are probably insufficient to foster the foundation of the Gastropoda from a mutation in a single veliger. Our results do support the suggestions of Thompson (1967) and Jägersten (1972), both of whom thought that torsion does not function effectively as a larval defense. It nevertheless remains conceivable that torsion confers other benefits to veligers; for example, torsion might aid in swimming (Underwood, 1972), and it is also possible that torsion protects veligers from adverse physical conditions. Pre-torsional veligers do retract within their shells, though they lack opercula.

It is also possible that untested or extinct predators are deterred by torsion while the predators we used are not. Although our selection of predator species was necessarily limited, we attempted to choose a diverse array of predators that are both common in neritic plankton and which feed by different mechanisms (see Pennington and Chia, 1984). Ctenophores, medusae, crustaceans, and planktivorous fish meet these criteria, though it remains problematic whether a predator such as *O. gorbuscha* had analogues in Cambrian seas. Though we cannot eliminate the possibility that extinct predators provided the selective pressure for torsion in veligers, there is little factual basis to support such an argument.

In contrast to Garstang's (1928, 1929) hypothesis, most other hypotheses regarding torsion postulate advantages during metamorphosis or for juveniles and adults (Lang, 1900; Naef, 1911; Yonge, 1947, 1960; Borradaile *et al.*, 1951; Morton, 1958, 1979; Allen, 1963; Morton and Yonge, 1964; Ghiselen, 1966; Purcheon, 1968; Jägersten, 1972; Underwood, 1972; Solen, 1974; Lever, 1979). If torsion is not a larval adaptation, one or a combination of these hypotheses probably explains its evolution within the Gastropoda. However, the selective pressures that have been suggested to favor torsion will remain speculative until further experimental work is conducted to examine the functional implications of torsion for gastropods.

LITERATURE CITED

ALLEN, J. A. 1963. Ecology and functional morphology of molluscs. *Oceanogr. Mar. Biol. Ann. Rev.* **1**: 253–288.

BORRADAILE, L. A., F. A. POTTS, L. E. S. EASTHAM, AND J. T. SAUNDERS. 1951. *The Invertebrata.* Camb. Univ. Press, Cambridge. 725 pp.

CALDWELL, M. E. 1981. Spawning, early development and hybridization of *Haliotis kamtschatkana* Jonas. Master's Thesis, Univ. Washington. 55 pp.

CARLISLE, J. G., JR. 1962. Spawning and early life-history of *Haliotis rufescens* Swainson. *Nautilus* **76**: 44–49.

CROFTS, D. R. 1938. The development of *Haliotis tuberculata,* with special reference to the organogenesis during torsion. *Phil. Trans. R. Soc. Lond. (B)* **288**: 219–268.

ELDREDGE, N., AND S. J. GOULD. 1972. Punctuated equilibria: an alternative to phyletic gradualism. Pp. 82–115 in *Models in Paleobiology,* T. M. Schopf, ed. Freeman, Cooper & Co., San Francisco.

FRETTER, V., AND A. GRAHAM. 1962. *British Prosobranch Molluscs.* Ray Society, London. i–ix: 1–755.

GARSTANG, W. 1928. The origin and evolution of larval forms. *Nature* **211**: 366.

GARSTANG, W. 1929. The origin and evolution of larval forms. *Rep. Brit. Assoc. Adv. Sci.* **D**: 77–98.

GHISELEN, M. T. 1966. The adaptive significance of gastropod torsion. *Evolution.* **20**: 337–348.

INO, T. 1953. Ecological studies on the propagation of Japanese abalone (genus *Haliotis*). *Tokai Reg. Fis. Res. Lab. Tokyo* 1–108.

JÄGERSTEN, G. 1972. *Evolution of the Metazoan Life Cycle, a Comprehensive Theory.* Academic Press, New York and London. 282 pp.

KNIGHT, J. B. 1952. Primitive fossil gastropods and their bearing on gastropod classification. *Smithsonian Misc. Coll.* **177**: 1–56.

KNIGHT, J. B., AND E. L. YOCHELSON. 1958. A reconsideration of the relationships of the Monoplacophora and the primitive Gastropoda. *Proc. Malacol. Soc. Lond.* **33**: 37–48.

LANDRY, M. R. 1978. Predatory feeding behavior of a marine copepod, *Labidocera trispinosa. Limnol. Oceanogr.* **23**: 1103–1113.

LANG, A. 1900. *Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere.* Fischer, Jena. i–iv: 1–509.

LEIGHTON, D. L. 1972. Laboratory observations on the early growth of abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. *Fish. Bull.* **70**: 373–381.

LEIGHTON, D. L. 1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. *Fish. Bull.* **72**: 1137–1145.

LEVER, J. 1979. On torsion in gastropods. Pp. 5–24 in *Pathways in Malacology,* S. Van Der Spoel, A. C. Van Bruggen, and J. Lever, eds. Scheltema & Holkema BV, Utrecht.

MILEIKOVSKY, S. A. 1974. On predation of pelagic larvae and early juveniles by adult benthic invertebrates and their passing alive through their predators. *Mar. Biol.* **26**: 303–311.

MORSE, D. E., H. DUNCAN, N. HOOKER, AND A. MORSE. 1977. Hydrogen peroxide induces spawning in mollusks, with activation of prostaglandin indoperoxide synthetase. *Science* **196**: 298–300.

MORSE, D. E., N. HOOKER, AND A. MORSE. 1978. Chemical control of reproduction in bivalve and gastropod molluscs, III: An inexpensive technique for mariculture of many species. *Proc. World Maricult. Soc.* **9**: 543–547.

MORTON, J. E. 1958a. *Molluscs.* Hutchinson Univ. Libr., London. 232 pp.

MORTON, J. E. 1958b. Torsion and the adult snail; a re-evaluation. *Proc. Malacol. Soc. Lond.* **33**: 2–10.

MORTON, J. E., AND C. M. YONGE. 1964. Classification and structure of the Mollusca. Pp. 1–58 in *Physiology of Mollusca, I,* K. M. Wilbur and C. M. Yonge, eds. Academic Press, New York, London.

NAEF, A. 1911. Studien zur generellen Morphologie der Mollusken. 1. Teil: über Torsion und Asymmetrie der Gastropoden. *Ergebn. Fortschr. Zool.* **3**: 73–164.

PENNINGTON, J. T., AND F. S. CHIA. 1984. Morphological and behavioral defenses of trochophore larvae of *Sabellaria cementarium* (Polychaeta) against four planktonic predators. *Biol. Bull.* **167**: 168–175.

PURCHEON, R. D. 1968. *The Biology of the Mollusca.* Pergamon Press, New York, 560 pp.

RUMRILL, S. R., J. T. PENNINGTON, AND F. S. CHIA. (in press). A stage-dependent predator avoidance response in larvae of the sand dollar *Dendraster excentricus. J. Exp. Mar. Biol. Ecol.*

SOLEM, A. 1974. *The Shell Makers, Introducing Molluscs.* Wiley-Interscience, New York. i–xii: 1–289.

STANLEY, S. M. 1982. Gastropod torsion: predation and the opercular imperative. *N. Jahrbuch Geologie Palaontologie Abhandlungen.* **164**: 95–107.

THOMPSON, T. E. 1958. The natural history, embryology, larval biology and post-larval development of *Adalaria proxima* (Adler and Hancock) (Gastropoda: Opisthobranchia). *Phil. Trans. R. Soc. Lond. (B)* **242**: 1–58.

THOMPSON, T. E. 1967. Adaptive significance of gastropod torsion. *Malacologia* **5**: 423–430.

UNDERWOOD, A. J. 1972. Spawning, larval development and settlement behavior of *Gubbula cineraria* (Gastropoda: Prosobranchia) with a reappraisal of torsion in gastropods. *Mar. Biol.* **17**: 341–349.

YEN, J. 1982. Sources of variability in attact rates of *Euchaeta elongata* Esterly, a carnivorous copepod. *J. Exp. Mar. Biol. Ecol.* **63**: 105–117.

YONGE, C. M. 1947. The pallial organs of the aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans. R. Soc. Lond. (B)* **232**: 443–518.

YONGE, C. M. 1960. General characters of Mollusca. Pp. 3–36 in *Treatise on Invertebrate Paleontology, I. Mollusca 1.* Geol. Soc. Amer., New York.

YONGE, C. M., AND T. E. THOMPSON. 1976. *Living Marine Molluscs.* Collins, St. James Place, London. 288 pp.